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Effects of forest degradation on Amazonian ferns in a land-bridge island system as revealed by non-specialist inventories

Gabriela Zuquim[1,2] | Maíra Benchimol[3] | Rafael Tonon[4] | Carlos A. Peres[5,7] | Danielle Storck-Tonon[6]

[1] Section for Ecoinformatics and Biodiversity, Biology Department, Aarhus University, Aarhus, Denmark
[2] Department of Biology, University of Turku, Turku, Finland
[3] Laboratório de Ecologia Aplicada à Conservação, Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Ilhéus, Brazil
[4] Independent
[5] School of Environmental Sciences, University of East Anglia, Norwich, UK
[6] Programa de Pós-Graduação em Ambiente e Sistemas de Produção Agrícola, Universidade do Estado de Mato Grosso, Tangará da Serra, Brazil
[7] Instituto Juruá, Manaus, Brazil

Correspondence
Gabriela Zuquim, Section for Ecoinformatics and Biodiversity, Biology Department, Aarhus University, 8000 Aarhus C, Denmark and Department of Biology, University of Turku, Turku, Finland.
Email: gabzuq@utu.fi

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Abstract

1. Tropical forests have been rapidly deforested and degradation worldwide has outpaced biodiversity field sampling. No study to date has assessed the effects of insular habitats induced by hydroelectric dams on Amazonian understory plants. Fern community responses to anthropogenic effects on tropical forest islands can be revealed at a faster pace by using simple and cheap, yet informative, protocols that could be applied by non-specialists.
2. This study seeks to both understand the drivers of fern and lycophytes assemblages on forest islands and investigate the relative costs and effectiveness of a simplified sampling protocol that can be applied by non-specialists.
3. Fern species were sampled by a non-specialist who photographed all ferns and lycophytes within seventeen 0.25-ha plots on 10 forest islands at the lake of Balbina Hydroelectric dam, central Amazonia. Sampling was carried out opportunistically during a field expedition planned to conduct tree inventories. As predictors, we used locally measured or GIS-derived descriptors of plot and landscape conditions. We used multivariate and linear models to further assess the influence of predictors on patterns of species richness and composition of ferns assemblages.
4. A total of 286 photographed individual ferns or lycophytes represented at least 23 species and 14 genera. The average number of taxa per plot was 6.1 in the islands and 14.3 in the mainland. The species pool found on islands was a nested subset of

the mainland fern community. Species richness was positively related to island size and negatively related to isolation and fire severity. Area, isolation and fire severity also significantly explained variation in community composition.

5. The relative cost of the picture-based fern protocol applied was very modest (only 4% of the total expedition budget), even compared to the typically low cost of alternative field campaigns.
6. We conclude that fern community structure in this forest archipelago was primarily driven by island size, isolation and fire disturbance. Moreover, we show that a simple sampling protocol carried out by a non-specialist can lead to inexpensive and highly reliable ecological data. This opens an avenue for crowdsourcing ecological fern data collections using a citizen science approach.

KEYWORDS
community ecology, Island biogeography, sampling protocol, tropical forest, understorey plants

1 | INTRODUCTION

Tropical forests have been rapidly deforested and degraded worldwide, with more than one-quarter of global forest loss driven by agricultural activities, mining or energy infrastructure (Curtis et al., 2018). Specifically in the Amazon, the world's largest tropical rainforest, an unprecedented expansion of hydropower dams has been implemented in the last decades, resulting in wholesale loss and fragmentation of pristine forests (Lees et al., 2016; Winemiller et al., 2016). Large hydroelectric projects established in lowland forests typically submerge vast areas, creating archipelagos of forest islands and inducing rapid biodiversity erosion (Benchimol & Peres, 2015b). Consequently, understanding how species diversity is shaped within highly fragmented hydro-reservoirs is of utmost importance to identify the mechanisms governing the persistence of newly isolated tropical biotas and propose sound conservation strategies.

Since the publication of MarArthur and Wilson's book in 1967 revealing the revolutionary Theory of Island Biogeography (TBI), area and isolation metrics became widely used by ecologists to evaluate their effects on patterns of species richness within forest fragments of the real world (i.e., embedded within human-modified forest landscapes [Laurance, 2008]). As predicted by TBI, the greater the island and shorter is its isolation to the nearby mainland, the higher is the number of species expected to occur, given the differential probabilities of extinction and colonization. Although several limitations of TBI have been shown, most studies conducted in hydroelectric reservoirs revealed a powerful area and/or isolation effects on the richness of a wide range of biological groups (Benchimol & Peres, 2021; Storck-Tonon & Peres, 2017; Yu et al., 2012). Yet, landscape predictors and habitat quality also revealed to be good predictors of species richness and therefore have been widely used by ecologists to scrutinize the diversity patterns in fragmented forest landscapes.

A growing number of studies have assessed the effects of fragmentation on plants in tropical reservoirs, mostly focusing on trees and lianas (Benchimol & Peres, 2015a; Jones et al., 2017, 2019; Yu et al., 2012). Patch-scale attributes (e.g. island size and edge-mediated forest disturbance) have been reported as the main factors affecting tree community structure. However, no study to date has assessed the effects of insular habitats induced by hydroelectric dams on neotropical understorey plants. Ferns and lycophytes (collectively known as pteridophytes) comprise a diverse, conspicuous and widely distributed group in the understorey of tropical forests and are well-recognized as a biological indicator of habitat quality (Salovaara et al., 2004; Zuquim et al., 2014). In undisturbed lowland Amazonian forests, soils are the main determinant of fern communities at several scales (Tuomisto et al., 2003; Zuquim, Costa, et al., 2009) and fern species richness tends to increase with soil fertility (Tuomisto et al., 2014). Yet, anthropogenic disturbances, including deforestation, and understorey fires alter environmental conditions and might exert a significant influence on patterns of species richness and composition of ferns and lycophytes on forest islands. The disturbance dynamics and potential source of propagules might play a major role, perhaps even overriding the original baseline conditions of environmental effects and fern community composition in lowland Amazonian forests.

Although biodiversity studies have been increasing across the Amazon basin, plant inventories and collections are still scant and geographically biased (Feeley & Silman, 2011; Hopkins, 2007; Schulman et al., 2007). Poor availability of field data in several Amazonian areas and forest types inhibits the unravelling of ecological processes, dynamics and threats. Conservation planners and ecologists may never have sufficient resources required to collect enough data to properly address conservation practice and science, especially considering the sheer size and species richness of Amazonia. A research agenda for the vast and megadiverse Amazonian region should include creative solutions in efficient biodiversity data acquisition.

A potential solution to mitigate the data gap problem is to outsource data collection to non-specialists. This can address the currently slow accumulation of species records and boost data availability (Dickinson et al., 2010). In addition, by involving non-academic members, it has an intrinsic value in raising ecological awareness and contributing to community capacity-building and education (Schläppy et al., 2017). For studies of charismatic animal groups, the division of labour between amateur observers and experts has already produced an enormous volume of quality data for some biological groups. For example, records obtained by citizen scientists represent 70% and 87% of the total mammal and bird records, respectively, in the Global Biodiversity Information Facility (GBIF) (Chandler et al., 2017). This is a consequence of citizen science campaigns that have occurred around the world and resulted in important societal and ecological contributions (ElQadi et al., 2017; Gonella et al., 2015; Laaksonen et al., 2017; Winterton et al., 2012).

In most tropical countries, citizen science campaigns are still rare, and citizen science is in its infancy. In the case of megadiverse systems, ecologically informative data could be collected by non-specialists if simple ecological protocols are available. Given the straightforward detectability of ferns, this group may be an interesting model to be promoted and assessed with the aid of non-specialists. Ferns are abundant in the understorey of most forests, and non-specialists usually clearly recognize a fern when they see one. Most of the Amazonian lowland ferns can be easily identified from photographs (Suominen et al., 2015) either by experts or the layman with the help of simplified identification tools (Zuquim et al., 2008, 2017). Equally important, ferns comprise excellent predictors of both soil properties and species composition of other floristic groups (Ruokolainen et al., 2007; Sirén et al., 2013; Zuquim et al., 2019). Therefore, a georeferenced photograph can be valuable and provide useful information about the prevailing environmental conditions at a forest site.

Here, we provide the first quantitative assessment of fern and lycophyte responses to the insular pattern of fragmentation caused by a mega hydroelectric dam in central Amazonia. We used an innovative approach of rapid sampling done by a non-biologist to understand the effects of patch, landscape and habitat characteristics as predictors of these understory plant assemblages across forest islands. In particular, we (i) investigate the influence of area, isolation, forest cover and fire severity on both species richness and composition, and (ii) discuss the relative cost and benefits of adopting a simple biological inventory protocol carried out by a non-specialist at poorly known tropical sites. This study is, therefore, two-folded and intends to both understand the ecological impacts of a man-made archipelagic landscape on a focal biological group and demonstrate that a rapid protocol that can be applied by non-specialists can lead to relevant ecological findings. We further provide evidence and guidelines on how opportunistic field data acquisition can be optimized to target areas ranging from poorly investigated sites to well-established vegetation monitoring programs to improve our understanding of drivers of plant community structure. This can, in turn, contribute to both enhancing ecological knowledge and propose sound conservation strategies to tropical forest landscapes.

2 | METHODS

2.1 | Study area and plot location

We sampled ferns and lycophytes (hereafter, ferns) within forest islands at the Balbina Hydroelectric dam archipelagic landscape of central Brazilian Amazonia. The 4437-km^2 reservoir lake was created following the impoundment of the Uatumã river by the Balbina Dam in 1987. This reservoir retains over 3500 variable-sized islands of primary sub-montane dense forest, although large patches of successional second growth occur on many islands as a result from post-damming old-growth tree mortality (Benchimol & Peres, 2015a). We conducted fern surveys on forest islands, which were spaced by at least 2 km apart and selected on the basis of forest area and degree of isolation, using Landsat ETM+ scenes (230/061 and 231/061; see details in Benchimol & Peres, 2015a). Fieldwork was originally planned to investigate tree dynamics in 17 islands, by conducting a re-census on 44 permanent forest plots. We subsequently decided to apply a rapid picture-based fern sampling protocol in 17 plots within 10 islands, but no additional financial resources were available for such sampling. All plots were located on islands within or adjacent to the ~940,000 ha Uatumã Biological Reserve, the largest reserve in this category in Brazil. Although islands are protected against hunting and logging, several islands had succumbed to ephemeral understorey fires during a severe El Niño drought in 1997, which mostly affected small-sized islands and induced marked changes in floristic composition (Benchimol & Peres, 2015a). The mean annual rainfall and temperature of the region are 2376 mm and 28°C, respectively.

2.2 | Plot design and fern picture-based sampling strategy

Fern inventories were carried out between September and October 2018 within 17 permanent 0.25-ha forest plots distributed across 10 land-bridge islands (Figure 1). The size of the islands varied between about 15 and 1450 ha. On each island, one to four plots were established, depending on island size. All plots were 250 m × 10 m, except for those on very small islands, which were 125 m × 20 m. The plots were primarily established in 2012 during adult tree inventories (see Benchimol & Peres, 2015a). Ferns were sampled covering the whole area of the tree plots. Plot dimensions were comparable to previous fern surveys conducted in the mainland continuous forest area surrounding the reservoir (Zuquim et al., 2012; red square in Figure 1). Plots were spaced by a minimum distance of 50 m from the nearest forest margin to minimize edge effects, and a minimum of 300 m from any other plot within the same island (Figure 1). In each plot, a quick picture-based sampling protocol was entirely carried out by a non-specialist (RT). This person had no previous experience in conducting fieldwork nor

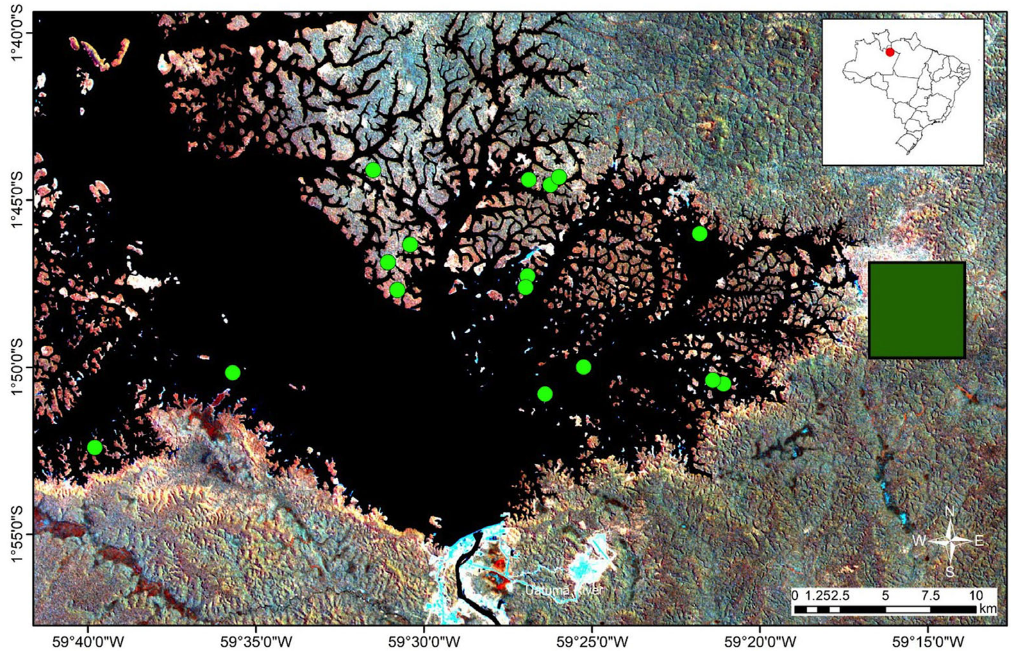

FIGURE 1 Study area showing the spatial distribution of the 17 plots (light green circles) distributed throughout the Balbina hydroelectric dam's landscape of central Brazilian Amazonia. Dark green square to the right of the image indicates the location of the mainland PPBio grid of plots sampled in 2007 ('Uatumã' plots in Zuquim et al., 2012). Background image: Landsat TM/ETM+ image composite 2000–2009 (Van doninck & Tuomisto, 2018); bands 4, 5 and 6 were assigned to the channels Red, Green and Blue, respectively

academic training in biological or environmental sciences and had amateur photography skills. He was originally earmarked to participate in the expedition to organize food supplies, transport and accommodation.

Inside each forest plot, photographs of all plant individuals that were recognized as a fern or lycophyte were taken by a non-specialist (RT). To become familiar with the flora, a photographic field guide (Zuquim et al., 2008) was consulted prior to the onset of fieldwork. Since most Amazonian fern species can be identified from photographs, all morphotypes found were photographed in the field using a Canon EOS 600D digital camera coupled with a common 50-mm lens. The specimens recorded were then compiled into plot-specific folders and digitally forwarded to a specialist (GZ) who identified the individual mostly to species level. To maximize logistical efficiency, ferns were sampled at the same time as the field team was conducting tree inventories on the same plots, although fern sampling was more time-efficient than tree sampling. Permits to work in the islands and in the Reserva Biológica Uatumã were granted by the Chico Mendes Institute for Biodiversity Conservation (ICMBio), in Brazil.

2.3 | Predictors

We took advantage of a pre-existing database that consisted of a set of locally measured or GIS-derived spatial metrics describing each survey site at the plot, patch and landscape scales (see Benchimol & Peres, 2015a for the description of all variables). From the full Balbina Island Biogeography Project database (Table S1), we pre-selected those variables that were least correlated (Figure S1). Whenever two variables were highly correlated (>0.70), we selected only one of those to be included as a predictor, according to our previous knowledge on island biogeography and plant ecology. The pre-selected variables were as follows: (1) Island area in hectares ($\log_{10}(x + 1)$; AREA); (2) Isolation measured as the shortest linear distance from each island to the mainland (ISOLATION); (3) Percentage of forest cover around the perimeter of each island (COVER), which was estimated using multiple-sized buffers (500 and 1000 m buffers). These sizes were chosen because they have already been used in previous studies (Benchimol & Peres 2015a, b) and enable for non-overlapping landscapes, which is indicated for the patch-landscape sampling design; (4) Percentage of pioneer tree stems (PPIONEER) among all trees inventoried within each plot, considering only adult trees ≥10 cm DBH (diameter at breast height); and (5) a metric of fire severity (FIRE), estimated as a composite ordinal score (0–3) of burn severity (based on charred trees and height of char marks on the bole of each tree) and burn extent across the plot, which was estimated by three independent researchers during previous tree surveys. No island plot fell in the category 0 (no fire). Only three plots were classified as category 2. To increase the number of plots per category and increase statistical inference power, we decided a posteriori to lump categories 0 + 1 (and then considered as *low fire intensity*) and 2 + 3 (*high fire intensity*). AREA, ISOLATION, and COVER were quantified using ArcView 10.1 (ESRI, 2011) and Fragstats (McGarigal et al., 2012), whereas PPIONEER and FIRE were measured in the field by a team of scientists based on data collected within established forest plots (see Benchimol & Peres, 2015a for further details).

In addition to the variables obtained from the pre-existing database, we extracted Landsat TM/ETM+ reflectance values from a Landsat imagery composite at 30 m for the scene that covers the Balbina lake area (https://etsin.fairdata.fi/dataset/1b32feb8-e297-4113-b91f-c58fff275039/data; file 60W_2.5S_2.5.tif). The Amazonian Landsat TM/ETM+ composite originally covers the entire Amazon basin and is based on satellite images for the period 2000–2009 (Van doninck & Tuomisto, 2018). To obtain a single value for each band per plot, we obtained the median value from a 60-m buffer from the centroid of each plot. This was done separately for each band considered in this study (Bands 2, 3, 4, 5 and 7). To summarize the spectral reflectance of each plot, we carried out a Principal Component Analysis (PCA) and used the value of the first axis for the plot as a predictor in the models (LANDSAT PCA_1).

2.4 | Data analysis

The multidimensionality of fern species composition across all insular forest plots was reduced using Principal Coordinates Analysis (PCoA) ordination based on presence/absence data and the Jaccard similarity index to build the similarity matrix. The first axis of PCoA was used in models as an independent descriptor of species composition to understand how this may respond to environmental predictors.

Considering that the effect of landscape variables on biodiversity depends on the spatial scale at which the predictor is measured (i.e. the so-called 'scale of effect', see Fahrig, 2013), we firstly performed Generalized Linear Models to identify which radius (i.e., 500 or 1000 m) was most appropriate to assess the effect of COVER on patterns of fern species richness and composition. We then selected the radius showing the highest correlation with species richness to be used in subsequent analyses. The 500 m was therefore chosen, as this yielded a slightly higher correlation with species richness than a buffer of 1000 m ($r = 0.49$ and $r = 0.37$, respectively).

Following the leading premises of island biogeography theory (MacArthur & Wilson, 1967), we first examined the effects of AREA and ISOLATION on fern species richness and composition using linear regression. We then investigated the influence of all predictors on patterns of fern species richness and community composition using Generalized Linear Mixed Models (GLMMs). In particular, we constructed models with all the five selected variables (AREA, ISOLATION, COVER, PPIONEER and LANDSAT PC1) and all possible combinations of subsets of these five. We used Poisson and Gaussian distribution link functions for species richness and composition, respectively. Since some islands had more than one plot, island was defined as a random effect to account for within island variation. We controlled for high levels of multicollinearity among variables by performing Variation Inflation Factors (VIF) (Dormann et al., 2013) using the 'HH' package (Heiberger, 2020) and excluded the least moderately redundant or collinear variables (VIF < 5). Models were subsequently ranked according to their Akaike Information Criterion (AICc), using the MuMIn R package (Barton, 2018) and selected (ΔAICc < 2.0) based on a multimodel approach and the AICc (Burnham et al., 2011). Explanatory variables were rescaled prior to modelling, using the *scale* function in R. We thus used a model-averaging approach using the MuMIn R package (Barton, 2018), which combines information from all candidate models to obtain model averaged parameter estimates.

To test the different responses of community composition to wildfires, we run a PERMANOVA ('*adonis*' function in R package *vegan* [Okasanen et al., 2020]) using the PCoA axis as response variables. In order to evaluate the extent to which the individual surveyed species were associated with plots that were affected by wildfires, we calculated the indicator species values using a modified IndVal metric (De Cáceres et al., 2010) for each species for each fire severity level. This analysis was done using the function '*multipatt*' from the *indicspecies* R package (De Cáceres & Legendre, 2009) and only species that occurred within more than three plots were included. All analyses were performed within the R 3.3.1 environment (R Core Team, 2018). The data are available at https://doi.org/10.5061/dryad.wstqjq2nq (Storck-Tonon et al., 2021).

2.5 | Comparisons with the mainland species

Finally, we compared the species list of each island with those from the same regional flora in the surrounding mainland. For this, we assessed a published data set ('Uatumã' sites; Zuquim et al., 2012) based on fern inventories conducted in 2007 within 29 quarter-hectare permanent plots of the Brazilian Biodiversity Research Program (PPBio [ppbio.inpa.gov.br]). The inventory was done by a fern specialist (GZ), who collected vouchers of the individuals and identified them at the INPA herbarium. Plots were spaced apart by 10 to 50 km from the nearest and farthest surveyed island, respectively (Figure 1). We compared the list of species observed in each environment accounting for the differences in the number of plots established in each environment (17 in islands vs. 29 in the mainland). To do so, we obtained the species list for 17 (out of 29) randomly selected mainland plots, which were compared with the species list obtained from the surveyed 17 island plots. This procedure was done iteratively 1000 times. It is important to note that plot sizes in both environments were the same. However, individuals were recorded only by pictures in the islands, whereas in the mainland, voucher specimens were collected and identified in the herbaria, resulting, in a few cases, in a higher identification resolution. For example, all the five *Triplophyllum* species found in the mainland were treated as a single taxon at genus level, and the congeners *Lomariopsis prieuriana* and *Lomariopsis japurensis* were also lumped together. For consistency, we harmonized the identification between island and mainland plots and some species that are difficult to distinguish from photographs alone were lumped species complexes in both data sets.

2.6 | Assessing the relative costs of a rapid sampling protocol

Ferns were opportunistically sampled during an expedition that originally aimed to resample trees within permanent plots established on forest islands of the Balbina Hydroelectric reservoir. The field team was formed by one researcher, one tree parataxonomist, one boatman and one logistical field assistant (RT). Whenever RT was not busy with field logistics, he was able to conduct fern sampling within the same permanent plots in which tree inventories were being carried out. Thus, in practice, the working hours that he allocated to the fern inventories optimized his multitasking role in the expedition. To estimate the relative costs of the fern protocol in relation to the total cost of the expedition, we first calculated the overall expedition costs for one person, by summing the costs of daily allowance, food and local transportation (boat driver and fuel for an outboard motor) for the whole team which was then divided by the number of participants. Daily allowance consisted of local labour market wages for 8 h of fieldwork including travel time. We then calculated the total number of hours that RT specifically allocated to the fern inventories, multiplied this value by the hourly wage labour cost of an assistant and defined this total as the cost of the fern sampling protocol. The relative financial cost was therefore defined as the cost of conducting the fern protocol divided by the total cost of the field campaign per person. Expenses were paid in Brazilian Reais (R$), but here we converted monetary values into U.S. Dollars (US$) using the commercial exchange rate at the time of the expedition (September 2018), according to the Central Bank of Brazil (https://www.bcb.gov.br/conversao).

3 | RESULTS

Considering all 17 plots, we obtained a total of 286 sets of pictures that represented different ferns or lycophytes, belonging to at least 23 species and 14 genera (Table S2). The most ubiquitous taxa in the data set were *Selaginella pedata*, recorded in 15 plots (88.2%), *Trichomanes pinnatum*, *Adiantum paraense/tuomistoanum* recorded in 14 plots (82.3%) and *Triplophyllum* sp. and *Lindsaea lancea*, both of which recorded in nine plots (52.9%). The other 18 species occurred in fewer than 50% of the sampled plots. Near half of the species (52.2%) occurred in only one or two plots.

3.1 | Fern responses to environmental and insularization predictors

3.1.1 | Fern species composition

The first PCoA axis ($PCoA_1$) explained 48% of the overall variation in floristic composition among plots. The $PCoA_1$ scores were then used in GLMM models as a response variable that summarizes the plot-scale species composition. Fire severity was the main predictor of species composition (Figure 2), but isolation was also included in the second best model (Table 1). The percentage of trees defined as pioneers and the spectral descriptor of each site (LANDSAT PCA_1) were not selected in the 'best' models as good predictors of floristic composition. Variation in species composition (as expressed by $PCoA_1$) was significantly correlated with both island size ($R^2_{adj} = 0.45$, $p < 0.001$) and isolation ($R^2_{adj} = 0.29$, $p < 0.001$).

3.1.2 | Species richness

When all variables were included in the GLMMs models, isolation was the strongest predictor of species richness considering model-averaging estimates (Figure 3a). Fire intensity and island size were also selected as good predictors in models with $\Delta AICc < 2.0$ (Table 1). Percentage of pioneer trees (PPIONEER) and the summary metric of land cover reflectance (LANDSAT PCA_1) were uninformative in the best models explaining species richness. There was a positive semi-log linear relationship between fern species richness and island size ($R^2_{adj} = 0.46$, $p < 0.001$; Figure 3b), and a negative relationship with island isolation ($R^2_{adj} = 0.43$, $p < 0.001$; Figure 3c).

3.1.3 | Community and individual species responses to fire severity in islands

Community composition varied along the plots (Figure 4) and the differences in composition among plots with low versus high fire severity were significant (PERMANOVA: $F = 4.614$; $R^2 = 0.21$; $p < 0.01$). Given that the history of wildfires was the main predictor of species composition, we sorted all species according to the fire severity gradient (Figure 5). Ten species were found exclusively on unburnt islands or those subjected to low fire severity. A total of 13 species were found in plots that had been moderately to heavily burnt. Of those, four were not observed in the low fire severity plots, but these species also occurred in mainland forest plots, which likely indicates this is an effect of the sampling rather than a habitat preference for disturbed sites. The indicator species analysis showed that the following species were significantly associated with unburnt or slightly burnt sites: *Lindsaea lancea* var. *lancea* (indicator value = 0.76, $p < 0.001$), *Polybotrya sessilisora* (indicator value = 0.69, $p < 0.05$), *Asplenium serratum* (indicator value = 0.60, $p < 0.05$) and *L. japurensis/prieuriana* (indicator value = 0.60, $p < 0.05$), whereas none of the species were associated with heavily burnt sites.

3.2 | Differences among sampled species richness in islands and mainland fern flora

When harmonizing and standardizing species identification between island and mainland plots (e.g. considering all *Triplophyllum* spp. as one taxa) and considering subsets of 17 mainland plots, seven taxa on average were exclusively recorded on islands, usually epiphytes that occur in the mainland but may not have been recorded in the mainland plots because those were sampled only up to 2 m high. Conversely, on average 36 taxa were observed in the mainland but not on islands (SD = 4, range = 21–42). A total of 23 taxa were observed across the 17 islands, and 58 taxa were observed in the mainland plots. Average

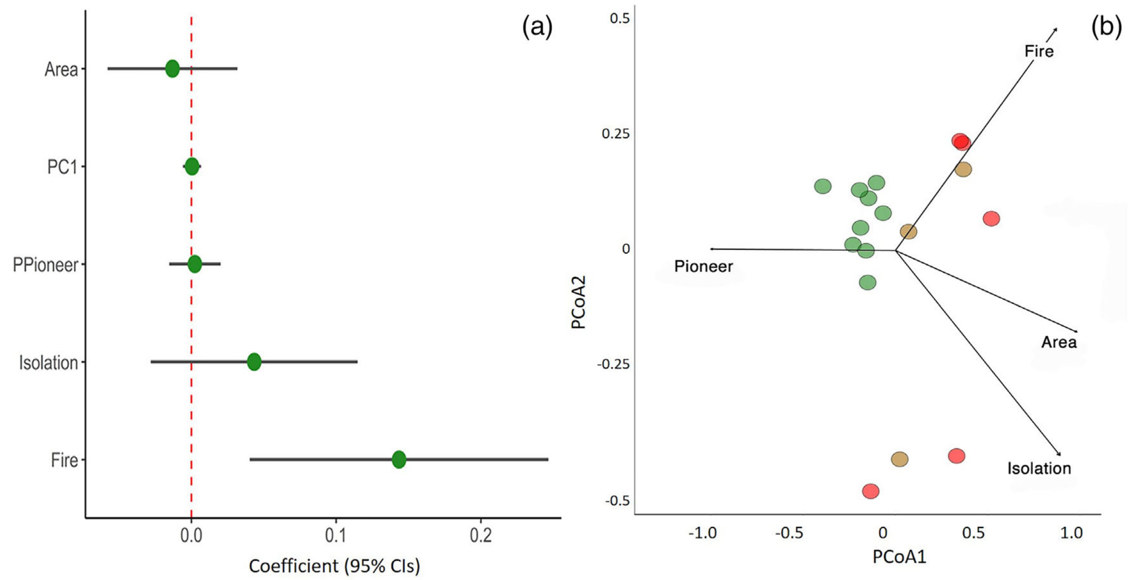

FIGURE 2 Predictors of fern species composition in 17 islands of Balbina hydroelectric reservoir, Brazilian Amazonia. (a) Results of model averaging of candidate models within AICc < 2, explaining the variation in fern species composition, summarized as the first PCoA axis. (b) Scatterplot of the two first fern species composition axes (PCoA 1 and 2); fire severity is represented by a colour gradient from green to red (low to high severity). The arrow sizes and directions are derived from the correlation of the variables with the PCoA values and are not related to the plot axis. Green-Red shades indicate the gradient of fire severity, from low (green) to high (red). Area, island area ($\log_{10}(x + 1)$); Isolation, distance to the nearest mainland continuous forest site; PPioneer, percentage of pioneer tree stems; Fire, Fire severity; PC_1, spectral signature of forest cover, defined as the scores along the first ordination axis of PCA analysis for LANDSAT bands 2–5 and 7

TABLE 1 Results of the Generalized Linear Mixed Models (GLMMs) for the effects of Area = island area ($\log10(x + 1)$); Isolation = distance to the nearest mainland area; Fire = fire severity on fern species richness and composition in 17 plots on islands of Balbina hydroelectric reservoir, Brazilian Amazonia. Only the best models are shown (ΔAICc < 2)

Response variables	Best models	AICc	ΔAICc	Akaike weights
Species richness	Isolation (−0.431)	76.7	0.00	0.28
	Isolation (−0.341) + Fire (−0.170)	78.2	1.51	0.13
	Isolation (−0.322) + Area (0.155)	78.7	1.95	0.10
Species composition	Fire (0.201)	2.4	0.00	0.44
	Fire (0.106) + Isolation (0.141)	4.3	1.94	0.17

species richness per plot was 6.1 (range = 2–10), whereas the average species richness in the 29 mainland plots was 14.3 (range = 4–27).

3.3 | Protocol for a non-specialist and added costs

Of the 294 individual plants photographed, eight were not a fern and were thus discarded. All individuals considered here could be identified to at least the genus level. In general, few photographs per individual were sufficient to yield identification to the species level (Figure 6). Individuals that could not be identified to species level belonged to the genus *Triplophyllum* (which can only be distinguished after checking indument characteristics under a microscope) and *Adiantum paraense* and *A. tuomistoanum* (because they are morphologically similar and were conservatively lumped into one taxon). Moreover, *L. japurensis* and *L. prieuriana* were also pooled because most individuals found were juveniles and the best distinguishing character for this growing stage—form and colour of scales in the rhizome apex—was not clearly visible in the photographs.

The field expedition required 17 days of fieldwork (excluding travel time), in which 44 plots were visited to conduct tree surveys. The estimated total cost of the campaign was approximately US$ 925/person. These costs included fuel for the boat (US$ 175/person) and food supplies (US$10/person/day) for all four team members (researcher, parabotanist, boatman and logistics assistant) and daily wages for three members. Daily wages varied from US$ 40 to 80/day depending on expertise. Concomitantly to tree surveys, the assistant was able to carry out fern surveys in 17 of these 44 plots to which he allocated a total of 25.5 (18.75%) hours of all paid working hours. Fern sampling time per plot was on average 1.5 h. In terms of project cost, the

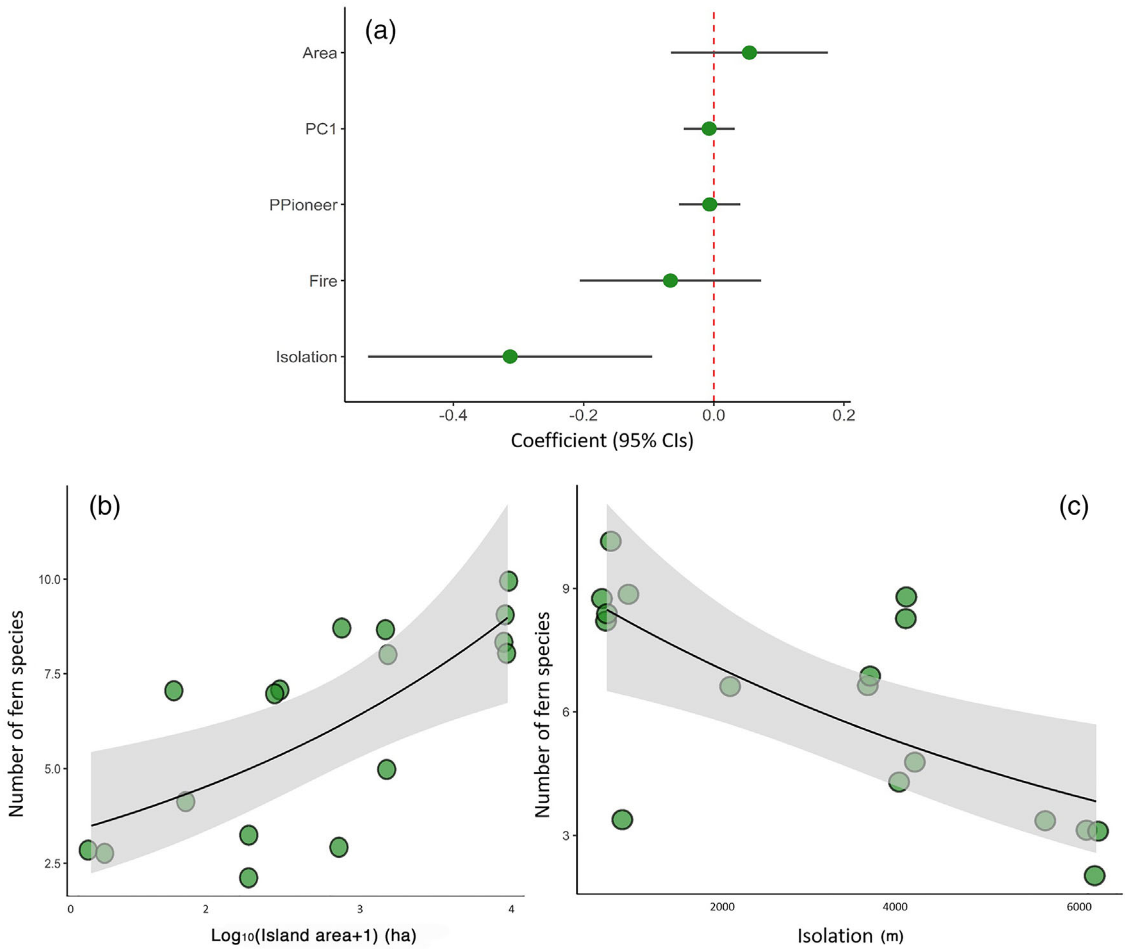

FIGURE 3 Predictors of fern species richness in 17 plots on islands of Balbina hydroelectric reservoir, Brazilian Amazonia. (a) Model averaging with candidate models within AICc < 2, for species richness of ferns. Mean ± 95% confidence intervals of regression coefficients obtained from GLMMs are presented. Relationships between fern species richness and area (b) or isolation (c) for linear models including these two variables as predictors. Area, island area ($\log_{10}(x + 1)$); Isolation, distance to the nearest mainland continuous forest; PPioneer, percentage of pioneer tree stems; Fire, Fire severity; PC_1, scores of first PCA axis for Landsat bands 2–5 and 7

protocol required a total of nearly three daily wages of the 17 daily wages paid for the logistics assistant in the expedition. In total, considering that transport costs would not be reduced if the fern surveys had not taken place, the added cost to implement this rapid inventory protocol encompassed only the hours that the logistics assistant allocated to the actual sampling and subsistence costs covering those 3 days. This amounts to a total of only about US$150 of the overall US$3700 cost of the entire field campaign. Including the fern sampling protocol into the campaign therefore represented only 4% of the total expedition budget.

4 | DISCUSSION

Our results show, for the first time, pervasive impacts of the insularization effects of a major hydroelectric dam on fern assemblages stranded on forest islands. In particular, distance to the nearest mainland and fire severity strongly affected patterns of species richness and composition, respectively. In fact, islands further from mainland continuous forest sites retained fewer species, whereas the community composition was mostly affected by the history of understorey (or surface) wildfires. Given severe personnel, time, and financial limitations, these findings were only possible due to our simple, yet standardized and informative, sampling protocol applied by an observer with no previous training in fern alpha-taxonomy. Our rapid sampling protocol based on individual photographs of ferns proved to be robust and greatly improve our ecological understanding of a poorly known area at a very low cost when compared to total costs of the expedition. Expanding the network of researchers adopting this protocol would produce relevant outputs for both science and society.

4.1 | Fern assemblages on land-bridge islands

According to MacArthur and Wilson's (1967) island biogeography theory, patch size and isolation are the key predictors of species

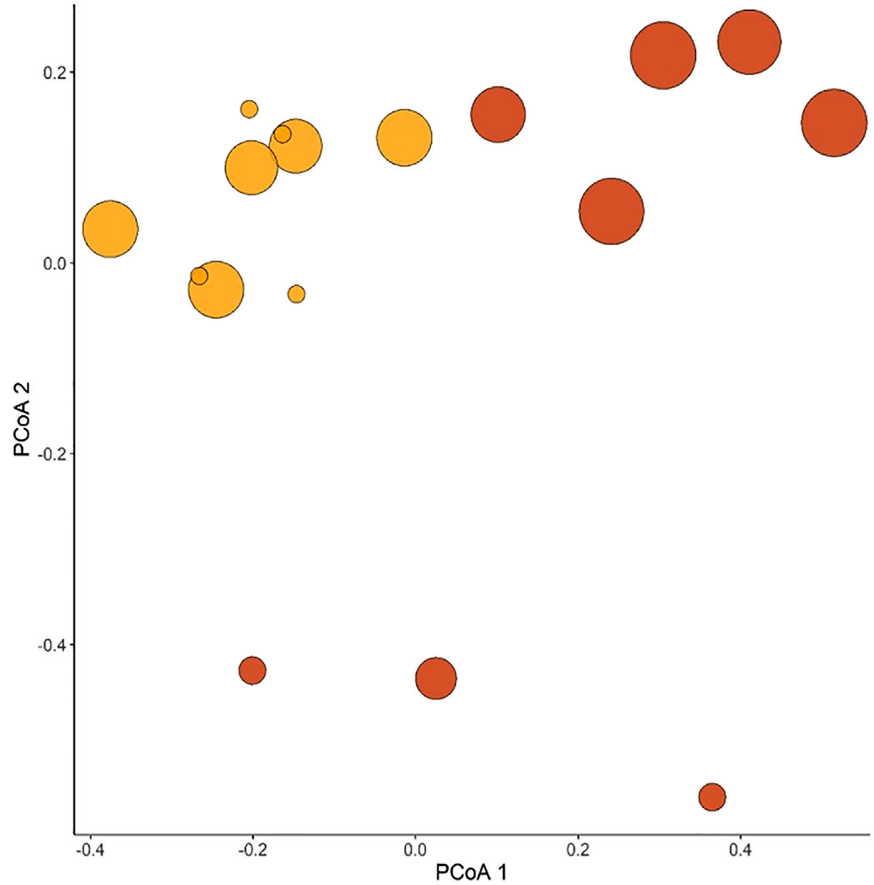

FIGURE 4 Results of Principal Coordinate Analysis (PCoA) of fern species composition in 10 islands of the Balbina lake, central Amazonia. The ordination was based on the pairwise matrix of plot dissimilarity using the Jaccard index. Island plots with low (orange) and moderate to high (red) fire intensity. Circle size is proportional to the minimum distance to the mainland

richness. In fact, a greater number of species was also observed on larger islands of the Balbina archipelago considering other plant (Benchimol & Peres, 2015a; Jones et al., 2017, 2019), vertebrate (Benchimol & Peres, 2015b; Palmeirim et al., 2018) and invertebrate taxa (Storck-Tonon et al., 2020; Tourinho et al., 2020). Furthermore, isolation greatly explained richness patterns. Islands closer to mainland forest sites can be colonized by a greater variety of fern species, which is largely explained by the propagule dispersal syndrome of pteridophytes. Likewise, distance to the mainland was the most important predictor of dung beetle defaunation and also negatively affected harvestmen assemblages in the Balbina archipelago (Storck-Tonon et al., 2020; Tourinho et al., 2020). Our results add further evidence that small islands, especially those farther from the mainland, safeguard lower taxonomic diversity compared to medium- to large-sized islands and mainland forest sites, providing further evidence that most forest islands smaller than 10 ha in this vast archipelago are highly depauperate in terms of biodiversity maintenance (see Benchimol & Peres, 2015b). It remains to be uncovered if the effect of isolation on fern communities is a direct consequence of dispersal limitation and slower re-colonization after disturbance or if it is a consequence of isolated islands being more rapidly affected by degradation (due, e.g., to more exposure to strong winds).

When all environmental variables were included in the GLMMs, both fire history and isolation appeared within the best models for species richness and composition. In the aftermath of a fire event, most species die out and recolonization mediated by propagules from the surrounding landscape may be stochastic (Hubbell, 2001). Ferns can quickly colonize areas after extreme disturbance events such as fires, landslides, hurricanes and deforestation (Walker & Sharpe, 2010 and references therein) because of the high wind-dispersal capacity of its propagules, known as spores, which are both highly abundant and long-lived (Perrie & Brownsey, 2007; Wolf et al., 2001).

The number of species sampled in the islands was around one third of that observed in mainland plots. The insular fern flora was a nested subset of the mainland flora, and several species that were common in the mainland were not found on islands. As discussed above, this is expected given that the insular flora at Balbina is typically depauperate because the vast majority of islands are small (Benchimol & Peres, 2015a). Another non-exclusive explanation for the smaller species pool found on islands is their overall spectrum of soil gradient compared to the mainland. Amazonian forest ferns exhibit strong soil affinity (Tuomisto et al., 1998; Zuquim et al., 2014) and the complex large-scale geomorphology of the Balbina region induces to high levels of edaphic heterogeneity (Figueir et al., 2014). As a consequence, fern species turnover in non-anthropogenic forests in our study area is primarily driven by edaphic properties (Figueir, 2014; Zuquim et al., 2014). Mainland plots spanned a large fraction of the overall soil gradient and contained species that are typical of the flora in both nutrient-poor and nutrient-rich soils (Zuquim et al., 2012). Although soil data are unavailable for our island plots, we primarily observed species described as

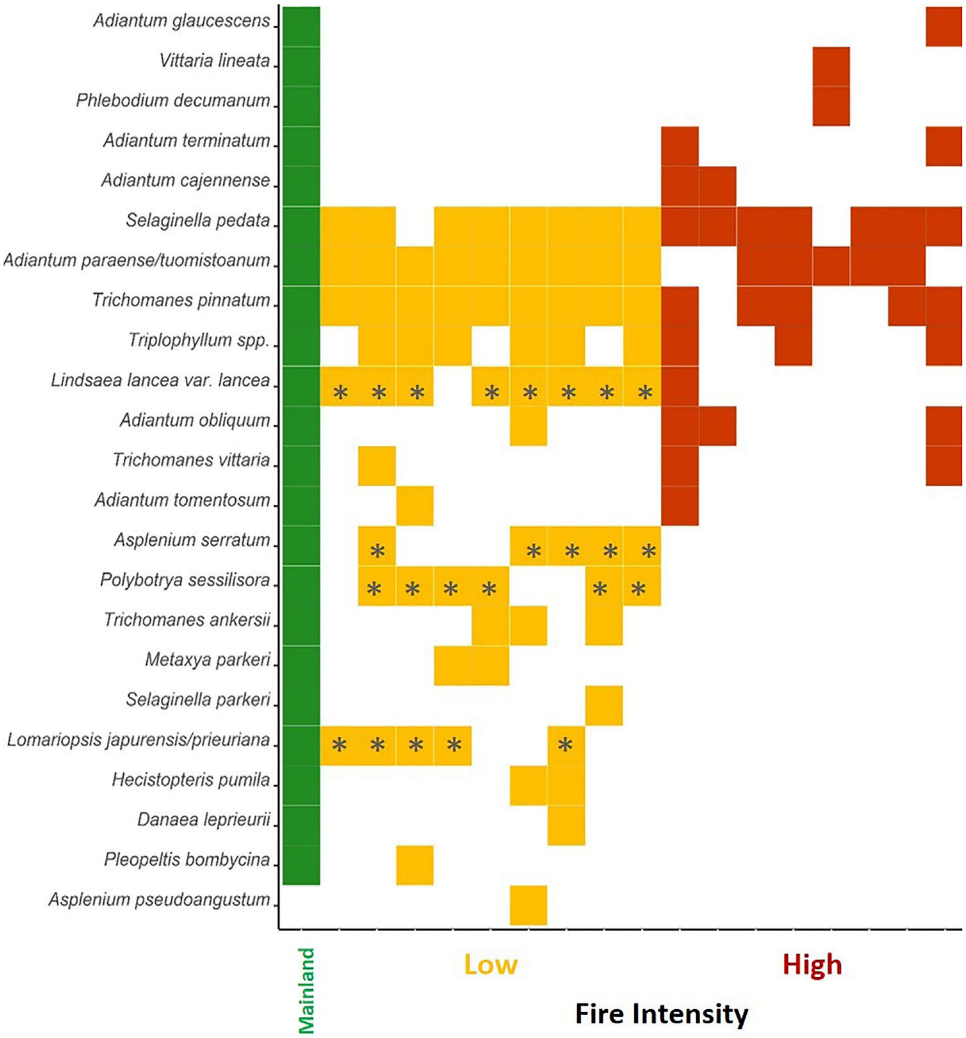

FIGURE 5 Site records of 23 fern species sampled across 17 plots on islands of Balbina hydroelectric reservoir and surrounding mainland forest sites (data from Zuquim et al., 2012). Species occupancies within plots are ordered according to understorey fire severity (low = orange, high = red). *Significant associations between fern species and fire severity adopting $p \leq 0.05$ as significance threshold

FIGURE 6 An example of a set of pictures of one individual sampled using the rapid picture protocol survey of ferns on the Balbina islands, central Amazonia, Brazil. (a) General aspect of *Asplenium serratum*. (b) Detail of the underside of the leaf showing leaf apex and sori morphology. (c) Detail of the basal part of the leaf and rhizome

poor-soil indicators (Moulatlet et al., 2017; Zuquim, Prado, et al., 2009), which suggests that the richer soil end of the gradient was not covered in the sampled islands.

4.2 | Effectiveness of rapid sampling protocol

In addition to the key ecological outcomes, our study revealed the benefits of using an image-based sampling protocol that can be implemented by non-specialists with almost no training. The basic previous knowledge required is to be able to recognize a fern as such and to be able to take a set of pictures that includes the general looking of the species and a few details. In terms of the costs of data acquisition in biological inventories, especially in remote or poorly known areas, this strategy can greatly benefit research and educational activities. The additional financial costs accounted for only 3.5% of the expenses in the planned expedition, which was initially designed to deploy tree surveys only. The fern protocol could be efficiently applied without significant increases in time and personnel allocated to fieldwork, and the overall financial cost of the expedition. This suggests that field efforts and costs in other large biodiversity research programs or networks such as RAINFOR (http://www.rainfor.org/), PPBio (https://ppbio.inpa.gov.br/en) and ATDN (http://atdn.myspecies.info/) could be optimized by using rapid photograph-based protocols such as the one applied here. As far as we are aware, this comprises the first successful initiative mounted to secure value-added floristic data in a tropical forest research program by optimizing non-specialist field assistants involving extremely low additional costs. However, each photograph was further identified by an experienced specialist, demonstrating that scientific researchers are also vital for the success of biodiversity monitoring protocols. Combining data acquisition by non-specialists and the critical scrutiny of the scientific community can expand the frontiers of ecological research and public engagement, ratcheting up multiple benefits (Dickinson et al., 2010).

By opportunistically delegating data collection to a non-specialist, we circumvented the data gap problem that often hinders ecological studies (Feeley, 2015; Hopkins, 2007). To achieve a quick, inexpensive and yet informative data set, we selected ferns as a model group, which are demonstrably good predictors of both soil properties and species composition of other plants in Amazonia (Sirén et al., 2013; Zuquim et al., 2014). Ferns could be reliably identified from photographs, and field observations were documented simply by taking digital photos of the plants with associated information of the plot location. Ideally, a good set of photographs for fern identification would include at least the general aspect of the plant, together with details on the upper and lower faces of the leaves from which diagnostic characteristics can be verified. These include growth habit, leaf (frond) desiccation, venation pattern, format, apex and sori if the individual is fertile. Other desirable characters to be recorded in photographs that may facilitate botanical identification include the rhizome. Ferns are abundant in the understorey of most closed-canopy forests, non-specialists can easily recognize a fern when they see one and building an effective search image for different forms of leaf morphology is quick. This ensures that scientists can obtain data from areas that specialists have rarely or never visited and opens an avenue for crowdsourcing ecological fern data collections using a citizen science approach.

In this study, the amateur photographer who sampled local fern assemblages did not identify any of the species in situ, and all fern photographs were identified to species level by an ecologist with vast experience in the Central Amazon. We are aware that this may have facilitated the identification process. Nonetheless, fern identification based entirely on photographs has already been used by other researchers (Suominen et al., 2015). Moreover, the availability of open-access, user-friendly online identification tools for Amazonian species (Zuquim et al., 2017), a global community of fern specialists (PPG I, 2016) and active members of picture-based platforms such as iNaturalist (iNaturalist.org), indicates that the identification step of the protocol used here is highly transferable to other geographic regions, regardless of the degree of previous local experience by alpha-taxonomists.

5 | CONCLUSION

We here showed that fern communities are driven by area/isolation and fire severity in a highly anthropogenic landscape and that the insular fern flora was a nested subset of the mainland flora. This demonstrates that the simple protocol applied revealed how island biogeography theory applies to fern communities in an anthropogenic system. Without a quick and cheap sampling protocol that could be opportunistically applied by a non-specialist, fern data collection would not have been possible, since fern sampling was not among the original aims of the field expedition. Therefore, the effects of forest degradation on ferns in an Amazonian land-bridge island system would have remained unknown.

This method can be used quickly, cheaply and efficiently by a non-biologist provided the motivation to census a plot systematically can be harnessed from volunteer or paid work. Field assistants and members of scientific expeditions responsible for logistics can carry out opportunistic data collection. Typically, a team carries out inventories in research programs where members could optimize data collections via quick photograph-based protocols such as the one applied here. As such, these key bioindicators can be easily added to already planned field expeditions, especially those occurring in vegetation plots/transects, without significantly increasing logistical costs.

In a rapidly changing world, finding innovative ways to collect informative data aids the scientific community to monitor and estimate how ecological communities may be impacted by climate change and climate–soil interactions, particularly if Amazonia becomes warmer and drier as predicted (Boisier et al., 2015). If applied by a wide public, simple ecological protocols can provide excellent-value field data, and thus, citizen scientists can help to improve species distribution maps, clarify how regional biodiversity is distributed and ultimately, provide background information for conservation planning (Chandler et al., 2017; Dickinson et al., 2010).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

GZ, DS-T and CAP conceived the ideas and designed methodology. DS-T, RT, GZ and MB collected the data. GZ, RT and DS-T processed the data. DS-T and GZ analyzed the data. GZ, MB, DS-T and CAP interpreted the results. GZ, MB and DS-T drafted the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All the data used are stored and freely available in Dryad Digital Repository at https://doi.org/10.5061/dryad.wstqjq2nq (Stork-Tonon et al., 2021). The data set includes the fern inventories and associated environmental predictors for 17 island plots and presence–absence inventories for 29 plots in the mainland.

ORCID

Gabriela Zuquim https://orcid.org/0000-0003-0932-2308

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